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A Contribution to the Biophysics of Podophyllum Petioles

BY

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A contribution to the biophysics of Podophyllum petioles

WALTER J. HIMMEL

(WITH FIVE TEXT FIGURES AND PLATES 30, 31)

The effect upon growth of such external factors as pressure and tension has been studied by a number of workers. While it is apparent that such agencies as gravity and wind may alter the shape of stems and in some cases have altered their internal structures, yet there is a question as to whether these agencies do alter the rate of growth and the rigidity of axial organs such as stems, petioles, roots, and hypocotyls. In this connection the mechanical forces involved in the growth and curvature of such structures deserve consideration.

A knowledge of the effect of pressure and tension on growth, and the mechanical forces involved in growth, is highly important not only in explaining the behavior of plants in their tropisms but also because during normal or pathological development the cells of a multicellular plant must affect each other not only by chemical secretion but also by the mutual stresses and strains within a growing tissue. This study therefore has a direct bearing on the problem of cellular interaction during ontogeny.

Hegler (1893) investigated the influence of tension upon growth by means of attaching a thread to the tip of the shoot, passing it over a pulley, and fastening it to a weight at its free end. He found that the tensile strength of such stems increased with increased tension. In repeating these experiments Ball (1904), a student of Pfeffer, found that the breaking strength of a plant does not increase in response to a gradually increasing pull.

Pfeffer (1893) later found that the primary root of a bean seedling embedded in plaster of Paris develops a pressure of 100 to 140 grams, often sufficient to burst the cast. Later with a spring-dynamometer he determined that the pressure thus developed overcame a resistance of 352.7 grams or 19 atmospheres. He also found that resistance applied in this way caused production of mechanical tissue.

Brush (1908) found that contact has a decided strengthening effect upon the tendril of *Passiflora caerulea* and by the addition of tension a still greater strength is obtained.

In working with the woody stems of *Robinia Pseudo-Acacia*, *Rhus glabra*, *Populus tremuloides*, and *Ricinus communis*, Pennington (1910) found that there was no increase in mechanical strength under the influence of longitudinal compression. In young herbaceous stems of *Helianthus annuus*, *Vicia faba* and *Phaseolus vulgaris* he found that the development of mechanical strength was somewhat retarded by longitudinal compression caused by a heavy weight. He states further that neither light weights nor heavy weights have any appreciable effect upon the growth and strength of herbaceous stems which have already formed a cylinder of woody tissue.

The application of other pressures than that of longitudinal compression have been studied in their effect upon growth. Andrews (1922) has shown that a water pressure of 600 atmospheres reduced the growth of *Zea Mays* seedlings on the average to only a small fraction of the growth rate of the normal plants.

Pressure seems to affect certain chemical phenomena and thereby to have some influence on the energy relations of tissues. Meldolesi (1921) found that the action of pepsin and trypsin upon blood albumen was influenced by a pressure of over one atmosphere of CO_2 and N_2. The reaction was most rapid at a pressure of 5 atmospheres, less at 10 atmospheres, but more than at one atmosphere. The hydrolysis of arrow-root starch by diastase was also influenced by pressure in the same way as was the action of pepsin and trypsin.

Not many studies have been made upon the amount of work done by plants in growth. Cremieu (1923) has recently estimated the work done in growth by oats. According to his calculations 125 kgm. of oat seed planted on a hectare of ground lift during their development into mature plants 1500 kgm. of seed and 300 kgm. of straw to a height of 0.6 m.

MATERIALS AND METHOD

The so-called sterile shoots of *Podophyllum peltatum* used in this investigation have been shown by Holm (1899) to be peltate leaves. They are very suitable for investigations on the effects

of pressure because of their firmness, the absence of lateral appendages, and because the region of elongation, unlike the delicate meristems of true stems, extends from near the distal end to near the middle of the petiole. In determining this region several petioles were marked at 10 mm. intervals and several at 20 mm. intervals. After several days the intervals were remeasured. Only those of the upper half of the petiole were found to have elongated. As an illustration of this elongation the following figures represent the successive intervals in mm. from the distal end of one petiole after several days growth: 20, 25, 29, 33, 21, 15, 10, 10, 10, 10, 10. A fourth advantage of this structure for such studies is that the weight can be placed directly on the top, without tying anything to the petiole.

The growing season of *Podophyllum* in any given locality continues only for a few weeks. It was found possible to secure actively growing petioles at other than the natural season both by breaking the dormancy early and by delaying development. The rhizomes bearing dormant buds were dug up in the summer and autumn and transplanted into flower pots. These pots were submerged in soil on the north side of a building and after exposure to considerable cold weather during the winter were brought into the greenhouse during the latter part of January, where the buds began to open within two weeks and in about another half week reached the stage suitable for use in the experiments. During February rhizomes were also chopped out of the frozen soil in the woods, covered with sand, and transferred to a refrigerator where they were kept at a constant temperature of about 1° C. until after the normal growing season had passed. As needed they were removed from cold storage, potted in flower pots, and placed in the greenhouse where they developed more rapidly than either the normal or the preseasonal material. Usually the buds of these plants opened in a day or two and were ready for experimentation within a week. In this way the length of the season was extended from 8 weeks to about 16 weeks.

In attempting to measure the mechanical forces involved in the growth and curvature of stems and stem-like parts of plants, and the maximum energy which the plant is capable of so expending, three groups of experiments were prosecuted. In the first group longitudinal pressure was exerted by placing on the

apex of the plant a light weight (about 25 grams) and periodically increasing this weight by equal increments as long as the plant continued to raise it. The rate of elongation was recorded twice daily, and after elongation had ceased, the bending strength of the petioles was determined and also the amount of work done in raising the weight calculated. In the second group of experiments the petioles of plants were flexed back and forth in one plane alternately on either side of the vertical. This process of repeated bending, which may be given the name of flexation, was continued for several days, and as the plant elongated, the amplitude of flexation was correspondingly increased. After elongation had ceased, the bending strength of the petioles was determined in the direction of flexation and in the plane at right angles to it. In the third group of experiments plants were placed horizontal, and the energy which they are capable of expending in tropic response to gravity was measured.

ELONGATION UNDER PRESSURE

Rate of elongation

The pots containing the plants were placed in large saucers filled with wet sand on a rotating table in the greenhouse. The average diameter of each petiole, both at tip and base, was determined both before and after the experiments. Glass tubing, the diameter of which was slightly larger than that of the petioles, was split and used for encasing the latter to prevent bending. It was put in place while the plants were still small, about 7 to 10 cm. high, and was held in a vertical position by means of a burette clamp and a ring stand. A glass thistle tube, the lower end of which had been closed with sealing wax, was placed upright upon the apex of the petiole and was held in place by allowing it to slide freely within a slightly larger piece of glass tubing held in place by a second burette clamp. The thistle tube was counter-balanced by an equal weight attached to a fine wire thread running over a pulley wheel. This pulley wheel was that of a Sach's simple auxanometer which was used for determining the amount of elongation at intervals during the growing period (plate 31, fig. 1). Controls were carefully selected, one for each plant, and were similarly set up, except that no weight was added as described below for the treated plants.

TABLE I

Rates of elongation in inches per hour for five plants and their controls

PRESSURE IN GRAMS	PLANT 550 AND ITS CONTROL			PLANT 554 AND ITS CONTROL			PLANT 597 AND ITS CONTROL			PLANT 599 AND ITS CONTROL			PLANT 681 AND ITS CONTROL		
	Hrs.	Exposed plant	Control plant	Hrs.	Exposed plant	Control plant	Hrs.	Exposed plant	Control plant	Hrs.	Exposed plant	Control plant	Hrs.	Exposed plant	Control plant
25	16	.0413	.0413	16	.0337	.0550							16	.0012	.0103
50	12	.0450	.0616	12	.0466	.0858	16	.0218	.0303	16	.0116	.0313	12	.0083	.0241
75	12	.0460	.0916	12	——	——	12	.0366	.1083	12	.0666	.1158	12	.0025	.0316
100	12	.0208	.0333	12	——	.0625	12	.0575	.1083	12	.0516	.1000	12	.0008	.0325
125	12	.0166	.0460	12	——	.0583	12	.0225	.1041	12	.0591	.1040	37	.0011	.0424
150	12	.0000	.0141	12	.0058	.0316	12	.0175	.0700	12	.0175	.0566	25	.0008	.0120
175	12	.0016	.0208	12	——	.0358	12	.0008	.0608	12	.0108	.0650	70	.0009	.0079
200	12	.0000	.0150	12	.0391	.0326	12	.0191	——	12	.0250	.0775	48	.0008	.0058
225	12	.0066	.0258	36	.0016	.0305	36	.0050	.0166	36	.0130	.0194	72	.0003	.0016
250	24	.0038	.0154	84	.0027	.0112	14	.0042	.0112	12	.0050	.0166	24	.0008	.0013
275	72	.0040	.0063				24	.0041	.0100	24	.0058	.0100			
300	36	.0025	.0091				24	.0041	.0250	24	.0179	.0233			
325							24	.0012	.0083	24	.0020	.0108			
350							24	.0008	.0050	24	.0025	.0025			
375							24	.0004	.0029	24	.0008	.0054			
400							60	.0003	.0060	61	.0006	.0054			

Either twenty-five or fifty grams of mercury were poured into the thistle tube of each plant treated. The needle of the auxanometer was then set at zero, and the plants were left to grow against this pressure. After 12 hours in some experiments and 24 hours in others, an equal amount of mercury was added. If the plant succeeded in raising this weight after a like interval of time, another 25 or 50 grams of mercury were added. If, however, the petiole had not raised the weight, the mercury was not added; but the plant was left undisturbed until the auxanometer registered an increment of growth at the time of the periodic readings. Mercury was thus added until the plant could no longer raise the accumulated weight.

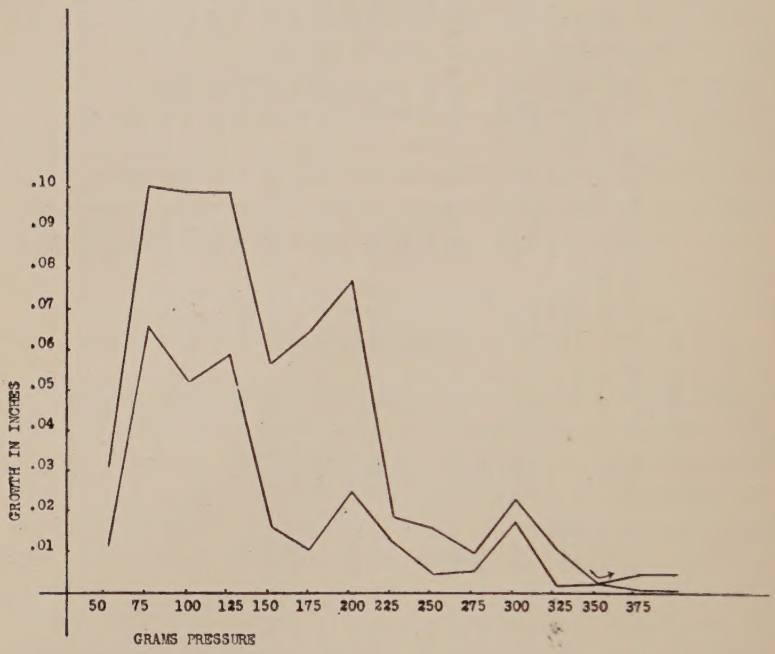

Fig. 1. Growth rates of plant No. 599 and its control represented graphically. Lower curve represents growth rate of exposed plant, upper curve rate of control plant.

The data in table 1 show that the rate of vertical elongation of the petiole decreases with increase of longitudinal pressure, but not in exact proportion. From figure 1, which represents

graphically the growth rates of plant no. 599 and its control, it is seen that, in general, an acceleration of elongation of the control is accompanied by an acceleration of elongation of the exposed plant as well. Likewise, a retardation of elongation of either is accompanied by a retardation of elongation of the other, indicating that the plants are responding similarly to external conditions. It will be seen also that the first pressure of 50 grams made considerable difference in the rates of elongation. The curves are farther apart after a pressure of 75 grams is applied, and the distance between them remains large until the larger pressures of 225 grams to 350 grams are applied, when the decrease in rate of elongation of the exposed plant does not keep pace with that of the control. After 225 grams of pressure were added and until a pressure of 400 grams was reached, the rates of elongation are nearly the same, and at 350 grams of pressure the two plants are elongating at exactly the same rate per hour for a period of 24 hours. This seems to indicate that the first effect of pressure is to decrease the rate of elongation but that later the plant responds in some way to this stimulus causing an increase in the rate and that the total effect of the pressure is markedly to increase the strength of the plant and the greater the pressure the more the strength is increased.

The rates of elongation for all of the plants used were averaged for each respective pressure. The values of these rates per hour, where the 25 gram increments were used, are shown in table 2 and the corresponding graph in figure 2. As in the curves for the individual plants described above, here too we find that the effect of the increase of pressure becomes less in retarding the rate of elongation.

From the data in table 2 the amount of work done by the plants can be calculated. This can be done by substituting in the following formula: $W = 2.54\ g\ \Sigma\ (wd)$, where W = work in ergs, 2.54 = gram-centimeter equivalent, g = gravity constant or 980.6, Σ = sum of products of w by d, w = weight added at respective intervals, and d = distance respective weights are moved. For the whole group of plants where the pressure was increased by 25 gram increments, the average total work done per plant was found to be 569, 782.76 ergs; and where the pressure was increased by 50 gram increments, the average total work done per plant was 438,367.42 ergs. There was no ap-

TABLE 2

Average growth in inches per hour for respective 25 gram increments of pressure

PRESSURE IN GRAMS	EXPOSED PLANTS	CONTROL PLANTS
25	.0218	.0276
50	.0231	.0425
75	.0274	.0736
100	.0209	.0596
125	.0173	.0644
150	.0065	.0319
175	.0037	.0257
200	.0072	.0191
225	.0029	.0113
250	.0018	.0073
275	.0025	.0061
300	.0049	.0119
325	.0017	.0095
350	.0016	.0037
375	.0006	.0041
400	.0005	.0057

parent relation between the total work done and the total weight lifted. The maximum work done by any one plant was 1,498,175 ergs.

The greatest weight which the plant could lift under the conditions of the experiments varies from 175 grams to 500 grams, the average being 300 grams. The amount of the periodic increments does not alter the total load which the plant can lift.

Bending strength

After the plant was no longer able to raise the accumulated weight, its bending strength was determined. For this purpose the flectometer (fig. 3) was devised. This instrument consists of a dial (A) marked off in degrees, in front of which is mounted a pulley (B) with a pointer (C). A silk cord passed over the pulley and suspended two counterpoised vials (D and D′). Above vial (D) a capillary tube (E), bent in the form of a double curve, connected above through a stop-cock with a wider tube partly filled with mercury. A second silk cord attached to the same vial (D) passed up over the pulley (B) and thence horizontally for a distance of about one meter to the petiole (F). It is

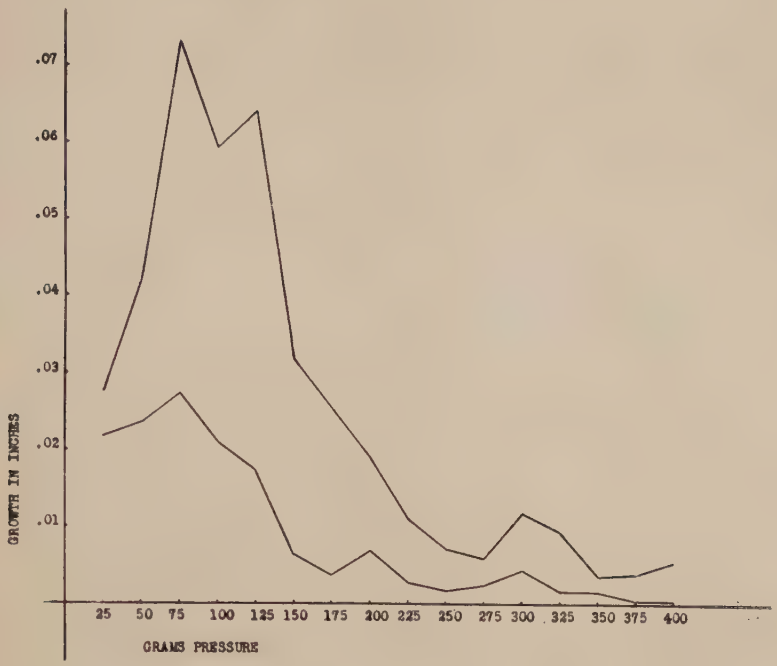

Fig. 2. Composite graph showing average growth per hour of all plants for periods of increasing pressures, based on data of table 2. Upper curve represents growth of control plants, lower curve the exposed plants.

attached to the petiole by means of a small wire hook. In order that the exposed and control plants might be tested in a comparable manner, the base of the petiole was held firm by a clamp attached at the same distance from the apex in the control as in the exposed plants, respectively. The pointer was set at zero and the stop-cock adjusted so that mercury dropped into the vial at the rate of 12 drops per minute. As the weight increased, the vial lowered, thus bending the petiole to an extent indicated by the pointer. The pointer was allowed to traverse the same angle for the exposed plant and its control. The angle chosen was a function of the length of the petiole. If the distance of the clamp from the apex was 19 cm., the angle traversed by the pointer was arbitrarily selected as 190°; if 15 cm., the angle selected was 150°; and so on. The weights of mercury required to bend the petioles to that angle were ascertained, thus measuring the bending strength.

Pennington (1910) used a scale mounted back of the tip of the inverted plant to which was attached a cord which passed over a pulley and bore a weight on its free end. He used the curvature of the stem as caused by a constant weight for meas-

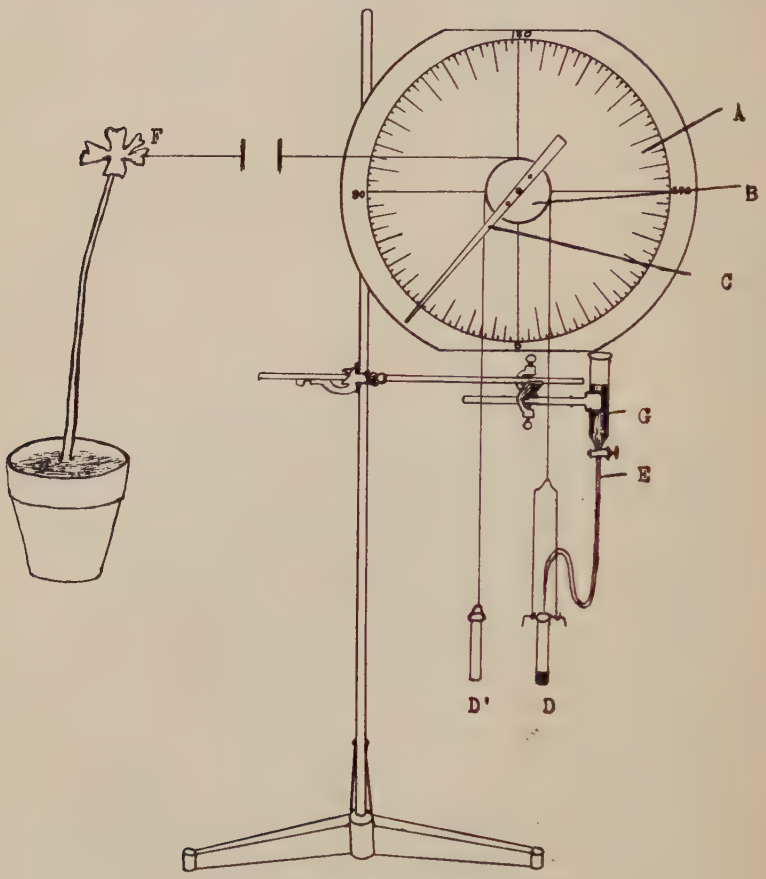

Fig. 3. Diagram of flectometer.

uring the resistance to bending. In our flectometer the weight is proportional to the length of the structure tested and is added very slowly, requiring all the way from twenty minutes to two hours. It furthermore seems that it is a better measure of the plant's bending strength to determine the weight required to bend it through a definite angle rather than to determine the

degree of bending by a certain weight added quickly. Plants vary greatly in their bending strength, and it is therefore unfair to apply a heavy weight to a weak plant or a light weight to a strong plant, as this may lead to considerable error in determining its real bending strength. Another advantage of the flectometer is that greater accuracy is attained by magnifying the movement with the pointer over the dial. A further feature of the flectometer is the comparatively long distance of the petiole from the pulley wheel. The very slight lowering of one end of the thread due to the bending of the petiole thus results in a negligible difference in the direction of the pull.

In table 3 are given the results of the bending strength determinations made on some plants exposed to longitudinal pressure and on their controls. In nearly every case the bending strength of the exposed petiole is greater than that of its control. In all except two cases, in which the bending strength of the control was greater than that of the exposed plant, the average diameter of the petiole was found to be larger. The average increase in strength for the plants investigated in this way was found to

TABLE 3

Bending strength of some petioles as determined by flectometer

PLANT NO.	EXPOSED PLANT				CONTROL PLANT		
	Length	Average diam.	Weight carried	Flectometer readings	Length	Average diam.	Flectometer readings
	cm.	*mm.*	*grams*	*grams*	*cm.*	*mm.*	*grams*
287	13.8	4.48	350	25.5629	17.5	4.84	30.0403
303	13.5	4.955	350	36.6566	13.5	5.10	33.3487
502	14.0	4.255	250	21.8802	14.6	3.81	16.3187
564	18.4	4.79	350	31.0081	19.9	3.585	17.3841
566	22.2	5.535	350	39.8913	23.7	5.57	31.0613
568	19.0	5.18	350	35.2213	17.0	4.44	15.7679
570	16.4	5.18	400	14.2509	25.0	4.07	14.6615
550	20.2	5.18	300	24.5395	24.5	3.45	13.8050
553	17.5	4.14	225	22.7851	22.0	4.025	15.5787
554	18.5	4.945	250	28.3726	25.0	4.0	14.2610
555	17.7	4.55	225	19.2204	28.3	5.245	29.9279
677	20.0	4.94	300	23.2325	19.5	4.28	21.6967
679	13.17	4.42	275	25.5953	22.5	4.29	32.9545
681	11.0	4.84	275	36.8603	17.0	4.18	16.9260
683	15.0	4.74	300	36.8185	14.0	5.37	37.2496
715	23.7	4.81	300	13.4910	28.4	4.78	10.2437
720	21.5	5.81	300	23.0787	16.8	5.56	22.3337

be 18 per cent. The average bending strength in terms of grams for the exposed plants was 26.9685 and for the controls it was 21.9740.

That this increase in bending strength is a permanent condition was shown by first determining it for a number of plants immediately after release from the pressure and again after the plants were left in the dark room for four days. The results were the same. If the resistance to bending had been the result only of turgidity, it seems that a decrease in turgor would follow release from the pressure and thus decrease in the bending strength.

Structural effects of longitudinal compression

The experiments described above show that longitudinal pressure during growth retards the rate of elongation and increases the bending strength of the petiole of *Podophyllum*. There seems to be, also, a certain structural modification resulting from longitudinal pressure. In this petiole there is an outer ring of bundles bounding a central pith and lying next to the inner margin of the cortex. Other bundles of the nature of leaf traces are distributed within the pith. Bordering the phloem of each bundle toward the exterior are thick-walled cells. Sections of the petiole of a control plant show very little of this mechanical tissue, whereas in sections of the petiole which grew against a final maximum pressure of 400 grams it is well developed. Furthermore, the walls of the parenchyma cells between the bundles also become thickened, and the cells are transformed into stereome. This difference is very evident in the sections of individual bundles highly magnified and shown in figures 1, 2, and 3 of plate 30. There also seems to be some difference in the organization of the xylem and in the character of the walls of the vessels.

EFFECTS OF FLEXATION

Some of the work on the effect of pressure and tension upon growth has been done by others with the view to explaining the eccentric growth of stems of Coniferous trees and the presence of "redwood." The trunks and branches of many trees have more wood on one side, and the annual rings on this thicker side are often reddish in color, resembling heartwood, the walls of the cells being much thicker and the wood much harder.

Burns (1920) exposed seedlings of pine to a bending motion to determine whether or not wind action could be the cause for the production of this mechanical tissue. He says that no "redwood" was formed nor did any eccentric growth take place as result of this bending. Koehler (1919), on the contrary, tied saplings in a circle and got red heart-wood on the inside. He attributes the formation of this "redwood" in this location to compression and not to a gravitation stimulus. Miss Gilchrist (1908), working mainly with sunflowers, reports that plants so swayed in one plane "are shorter and thicker" than control plants, that the "diameter in the plane of swaying is greater than that at right angles," that the "xylem in the plane of swaying is greater than in the transverse plane," that "a greater amount of xylem is produced than in stems of controls," that "the rigidity is greater in the diameter in the plane of swaying than in transverse diameter," and that "swaying 'in the wind' produces greater eccentricity." Hartig (1896), observing the effect of wind on trees, believed that longitudinal pressure on the cambium caused the production of "redwood." Later, however, (1901) he concluded that gravity may also act as the stimulus. Cieslar (1896) attributed the formation of "redwood" to a pressure stimulus as a result of bending young spruce trees. Ursprung (1901) maintained that it was a compression-strain stimulus resulting from the weight of the structure and the action of wind that caused the distribution of radial growth. Kny (1882) accounted for this one-sided increase in the growth of tree trunks on the basis of one-sided leafing of the tree causing one side to be heavier than the other. Growth is thus inversely proportional to the external pressure exerted upon the growing cells. Wiesner (1892) also attributed eccentric growth to unequal size and distribution of the leaves. DeVries (1876), by winding twine around stems, concluded that the presence of annual rings results from greater bark pressure at some seasons of the year than at other seasons. Krabbe (1884), however, proved that the bark pressure is never great enough to retard growth. Wortmann (1887) found that the collenchyma of the cortex of bandaged plants became greatly thickened. He attributed this to the fact that these cells could not reach their normal surface tension. Detlefsen (1882) also attributed eccentricity to bark pressure. Newcombe (1895) concluded that

the formation of mechanical tissue is not always caused by mechanical forces but calls the responses self-regulatory phenomena. Keller (1896), in considering the strengthening of the fruit-bearing axis, held that it is not due to tension because of the weight of the fruit nor because of the fruit-bearing itself, but that it is the change in direction of the axis which causes the anatomical changes. Pieters (1896), on the other hand, found that lignification of cell walls and increase in cells go hand in hand with fruit development. Vöchting (1902) found no increase in mechanical tissue in weighted sunflowers, some of which had been decapitated. In Savoy cabbages, all of which were decapitated, he found only a slight increase in mechanical tissue, but this was not proportional to the weights used. By removing the flower buds, he greatly retarded the formation of mechanical tissue in these plants. Subsequent addition of weights did not cause the mechanical elements to reappear. But when he grafted another stem onto the decapitated one, the mechanical tissue again began to form, although this additional weight was much less than the weights which he fastened to the decapitated stem.

In my experiments with *Podophyllum* petioles a device called the flector was constructed for bending the petioles back and forth in one plane. This consisted of a bicycle wheel driven by a small electric motor. To the wheel was eccentrically attached a stiff wire about five feet long, which was made adjustable on the wheel so as to increase or decrease at will the amplitude of the bending. This wire was held horizontal and at any desired elevation above the table by having it pass over adjustable wheels. The tips of the petioles were fastened along the side of the wire by cord so that they would be pulled first in one direction and then in the opposite. To avoid injury to the petioles, the cord was looped about a rubber band cut from tubing, slit open, and placed about the petiole just beneath the peltate blade.

Thirty-one plants were set up in this manner when they were about three or four inches tall, the extent of bending being only about two inches. The amplitude of bending was increased from two inches to about eight inches during the period of growth which lasted for a week to ten days. As soon as the petioles reached their maximum elongation, their bending strength in

two planes was determined by means of the flectometer, one plane being the same as that of the bending by the flector and

TABLE 4

Bending strength of plants which were flexed back and forth, and of controls for some of them

BENDING STRENGTH IN PLANE OF FLEXATION	BENDING STRENGTH AT RIGHT ANGLES TO PLANE OF FLEXATION	PERCENTAGE INCREASE	BENDING STRENGTH OF CONTROL PLANTS
grams	*grams*		*grams*
13.4177	14.5611	7.8	
24.4600	25.1233	2.6	
18.2003	18.9775	4.0	
16.0513	18.7273	14.0	
36.2526	38.0660	4.7	
15.9204	19.8324	19.7	
16.6287	16.9017	1.5	
28.4787	32.6488	12.7	
13.6571	14.7405	7.3	
17.6905	19.5478	9.5	
31.3711	37.1264	18.0	
14.8031	14.7245	.5	
34.1945	34.7887	1.7	
15.9371	19.9948	20.0	
11.9029	15.1808	21.0	
9.9481	10.1181	1.6	
16.4048	18.8279	12.8	
23.9100	28.9750	17.0	
14.9889	18.1944	17.0	
13.7554	15.4380	10.8	
10.0909	11.7310	14.0	
15.6587	18.4587	15.0	
8.0054	9.3630	14.5	
20.9037	28.6600	27.0	15.3924
16.8190	24.3812	31.0	21.7313
9.7771	18.2596	46.0	17.5165
30.7186	34.7196	12.0	18.3255
14.7183	16.7846	12.0	18.3094
22.0045	27.6760	20.0	20.1090
30.8175	38.7051	20.0	21.1216
19.4123	24.4924	20.0	14.6061
Average 20.4194	23.3523	14.0	18.3889

Increase over controls (based only on plants where controls were used): in plane of flexation, 12 per cent; at right angles to plane of flexation, 40 per cent.

the other at right angles to it. In table 4 is given the bending strength of these plants together with the bending strength of some of their controls. The bending strength of these plants, when determined for the same direction as the plane of flexation, was found to increase 12 per cent over that of the controls; but in the direction at right angles to this plane of flexation the increase was 40 per cent. This shows that, in *Podophyllum* at least, flexing motion results in an increase of bending strength. In all cases, except one, the bending strength at right angles to the plane of flexation was found to be greater than that in the plane of flexation. The maximum difference was 46 per cent and the average was 14 per cent.

The effect of flexation upon the bending strength of the plant is here seen to be approximately the same as that of longitudinal pressure. Here, however, the increase in the resistance to bending may be the result of the production of mechanical tissue or of a modification of form of the petiole. The length in mm. of the maximum diameters in the two planes was determined for ten plants as follows:

Same plane:	4.90	5.64	5.40	6.60	6.00	4.84	4.92	4.80	5.43	4.53
Right angles:	4.94	6.48	5.34	6.60	6.34	4.97	5.35	5.25	5.82	4.84

This gives an average maximum diameter in the same plane as flexation of 5.306 mm. and an average maximum diameter at right angles to the former plane of 5.5593 mm., showing a difference of .287 mm. This result of flexation in producing a difference in the diameter of the petiole may account for the difference in bending strength, although this evidence cannot be considered as being conclusive.

MEASUREMENT OF THE ENERGY OF GEOTROPISM

The force exerted by a petiole of *Podophyllum* in elongating vertically has been measured above. The force required to bend the petiole has also been ascertained. It now remains to be determined whether a stem or petiole in curving is capable of exerting more force than that which is just required to bend it. This can be done by finding the lifting power of such an organ during geotropic curvature.

Many workers have attributed geotropic curvature to the effects of pressure and tension upon growth. Ricome (1920),

supports the theory that negative geotropism may be due to the weight of the terminal portion of the plant causing a compression below which stimulates growth and a tension above which retards it. This pressure may not be due to the weight of the tissues, but it may be an increased osmotic pressure, as suggested by DeVries (1880). He concluded that gravity produces an increased osmotically active material in the cells of the lower side. Cielsielski (1872) observed a difference of the sap on the opposite sides; the cells of the convex-becoming side contained a thin watery protoplasm, and the cells on the side becoming concave had a denser and more opaque plasma. Kohl (1894) found in the sporangiophores of *Phycomyces* that in geotropic stimulation the plasma of the concave side became much thicker and that of the convex side thin and watery. On the other hand, Hilburg (1881) found that osmotic pressure of the concave side of leaf joints and stem nodes of various plants is greater than that of the convex side. Wortmann (1889) did not think that osmotic pressure had anything to do with geotropic curvature, since he could find no difference on the two sides. He thought that the thickened plasma on the concave side thickens the cell membranes on that side, making them less elastic than those of the convex side. Copeland (1900) found no difference in osmotic pressure on the two sides of stems split lengthwise and stimulated geotropically four days. Kersten (1907), using the plasmolysis method, also was unable to find any change in the osmotic pressure on the two sides. Miss Schley (1920) found that the osmotic pressure is greater on the convex side during the geotropic response, rising during stimulation and reaching a maximum at or before visible response, and decreasing as the response nears completion.

Czapek (1902) explained the response on the basis of chemical changes affected by the geotropic stimulus. Kraus (1879–1884) observed a rise in the percentage of reducing sugars and a diminution of acidity, especially in the under surface of a shoot placed horizontal. Any chemical change leading to a change of osmotic pressure would give similar results. A further evidence that a chemical change takes place is afforded by the observations of Chapman, Cook, and Thompson (1924), who found that with a concentration of CO_2 above 40–45 per cent growth ceases and with it all responses to gravity.

Haberlandt (1900) and Němec (1902) both attributed geotropic response to the settling of bodies in the plasma in a manner similar to the otoliths of animals. Zaepffel (1921) made a detailed experimental study of geotropism in the various parts of seedlings of certain grasses and concludes that movement of the starch grains disturbs the equilibrium between starch grains and the products of their hydrolysis, giving a difference of osmotic pressure which causes unequal growth of upper and lower parts of the cell. Němec (1902), Zollikofer (1918), and others found that in certain plants statolith starch disappears when placed in the dark and with the disappearance of the statolith starch also goes the ability to respond to the stimulus of gravity. Small (1920) and Bose (1920, 1921) assumed that the particles which settle carry electrical charges thus setting up a difference in potential within the cells. This increases the permeability to ions and conductivity in the upper side of the petiole more than in the under side. It also gives greater relative turgor on the under side, greater growth and therefore curvature upwards. They have been opposed in their theory by Blackman (1921) and Snow (1921) and also by Cholodny (1923). Blackman and Snow contend that an electrical potential great enough to produce the results which Small and Bose assume could not result in this way. Cholodny admits only the assumption of Small that electrically laden particles settle to the bottom of the cell.

For my experiments an instrument was constructed which automatically dropped a small weight into a container attached to the tip of the petiole, every time it raised the distance of a millimeter or less, thus pulling it back to its original position, that is, keeping the plant continuously horizontal. A kymograph records the time when each weight is dropped. This instrument may be called a tropograph.

The plant (fig. 4) was placed horizontal; the petiole encased in split glass tubing which was clamped firmly in position. Attached by a fine wire hook inserted in a loop of braid over the end of the petiole, a silk thread suspended a glass vial (B). This vial was counterbalanced by another (B′) over pulley D. In order to make certain that the braid did not slip away from the tip of the petiole, a short piece of thread was passed back of the braid just beneath the petiole, out through the deep clefts of the leaf and tied at the outside. Thus, when the plant was in

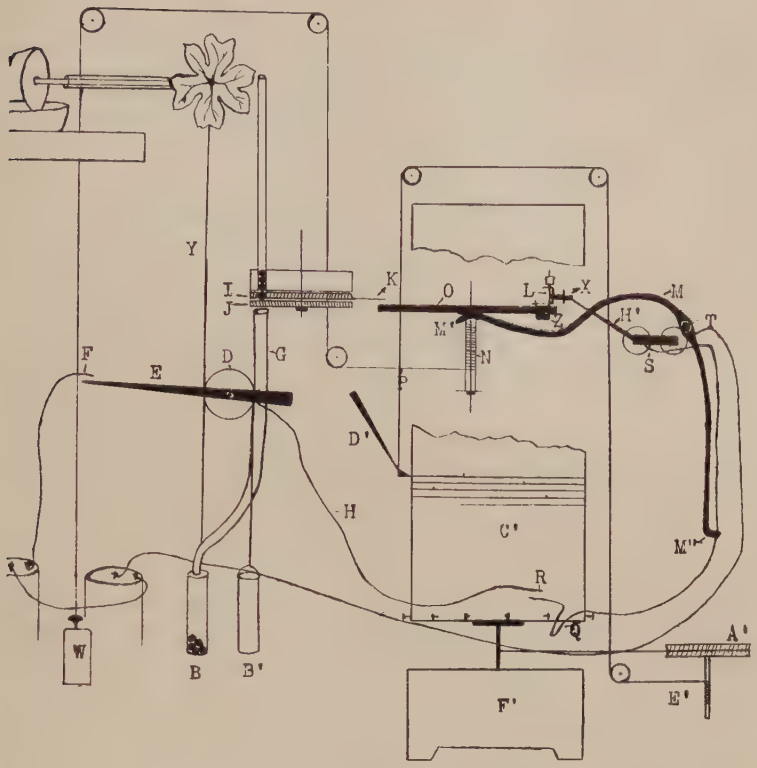

Fig. 4. Diagram of tropograph.

position, practically no weight was sustained by the petiole itself except the fine silk thread and the braid. The weight of the petiole was borne by the glass tube. Above the pointed end of arm (E) a copper wire was located connecting with four dry batteries in series. From its broader end a second wire connected with an electro-magnet (S) which operated a shot-dropping device; this magnet in turn was connected with the batteries. When the plant was placed in position, the pointed end of the arm was only 1 mm. or less from the wire (F). As the petiole rises, its movement is magnified five times at the tip of the arm. Only a very slight movement of the petiole therefore causes the circuit to close at (F) and by a mechanism, described below, a steel shot 4.5 mm. in diameter and weighing .3471 gram dropped through the tube (G) into the vial (B). In most

cases the weight of this single shot was sufficient to break the circuit. After a short period the petiole rose again and once more closed the circuit, causing another shot to drop into the vial. By a continuation of this process the petiole was kept from bending upwards while for a time it continued to increase the load which it was carrying.

For the dropping device an electro-magnet was mounted so that its arm (H′) extended to a catch (X) which prevented a disc (O) from rotating. On the lower portion of the axis of this turn-table (N) was wound a cord which passed over pulleys and suspended a weight (W). Beside the disc (O) two circular brass discs (I and J) were mounted closely one above the other, the lower one fixed, and the upper one movable on the central vertical axis. Over a hole through the upper disc was attached a glass tube containing a column of shots the lower one of which rested on the lower disc. At another place in the lower disc the same distance from its center was a similar aperture beneath which was the tube (G) leading to the vial (B).

When the electro-magnet was charged, it opened the catch (X), which allowed the disc (O) pulled by the weight (W) to rotate. An arm on this disc (O) engaged a lever (K) on the upper disc (I), causing that disc to rotate a short distance, carrying the single shot in the aperture to a position over the aperture in the lower disc (J) through which it fell into tube (G) and thence to the vial. A spring drew the lever (K) back to its former position allowing another shot to fall into the hole of the upper disc. The disc (O) was prevented from rotating again by the catch (X), which was not released until the electro-magnet was again charged. This could not happen for at least one minute, due to a second break in the circuit (R). At this point was placed a kymograph bearing a row of pegs at the base of the drum. As the drum revolved the pegs moved below the wire (Q) and raised it sufficiently to make contact again. These pegs were so spaced as to make contact at one-minute intervals, thus allowing the plant to return to equilibrium after each shot was dropped. A heavy wire (M) was so mounted near the electro-magnet that a projection (Z) on the underside of the turn-table (O) struck the end of the wire, thus breaking the second contact. Near the kymograph was placed a pulley (A′) turned by means of a belt connected with the shaft of the kymograph.

To the axis of the pulley was attached a fine silk thread which wrapped around it. This thread suspended a stylus (D′) which drew a spiral line on the kymograph, as it steadily raised by the thread wrapping around the pulley. When a contact was made, the arm (H′) of the electro-magnet was moved and the stylus was caused to move vertically, making a jog in the spiral line and thus indicating when the shot was dropped.

At first some difficulty was encountered when some of the petioles underwent torsion. When this occurred, the petiole would bend toward the right or left, depending on the direction of the torsion. This was overcome by mounting two small pulleys, one on either side of the tip of the petiole. A silk thread was attached to the braid over the petiole and passed over the two pulleys and downward past two other pulleys mounted close together and then attached to the vial. Thus it made no difference if the pull of the petiole were lateral or vertical; the circuit would be closed just the same, resulting in the shot being dropped into the vial.

From the kymograph records the number of shots dropped per hour was calculated and checked with the number of shots in the vial at the end of the experiment. The shots dropped in successive hours were for six plants as follows:

												Total
1:	17	6	6	14	11	9	7	1	—	—	—	71
2:	34	11	6	12	17	12	6	—	—	—	—	98
3:	16	9	9	9	11	14	14	10	8	—	—	92
4:	9	5	7	6	10	10	6	—	—	—	—	53
5:	3	2	1	5	3	4	4	4	4	4	3	37
6:	23	9	14	13	10	5	6	4	4	4	—	92

The reaction time was found to vary from 24 minutes to 88 minutes, with an average of 57 minutes. It was also found that the maximum load which the plant can lift in this manner ranges from 11.451 grams to 66.553 grams, with an average of 32.804 grams.

It is seen from these data that in nearly every case the number of shots dropped during the first hour is relatively large. There is a decrease in the number of shots dropped during the next hour, this decrease being larger in some cases and smaller in others. During the third hour the number of shots dropped may increase, or this increase may not take place until the third,

fourth, or fifth hour. But in every case there is a second maximum following the first maximum of the first hour. In several cases there was a third maximum.

In figure 5 are plotted the smooth curves for the total load at the end of each hour for four of the plants. In this figure the first part of the curve is convex rising rapidly. This represents the large number of shots dropped during the first hour. During the second hour the increase in the load slows up a bit. This

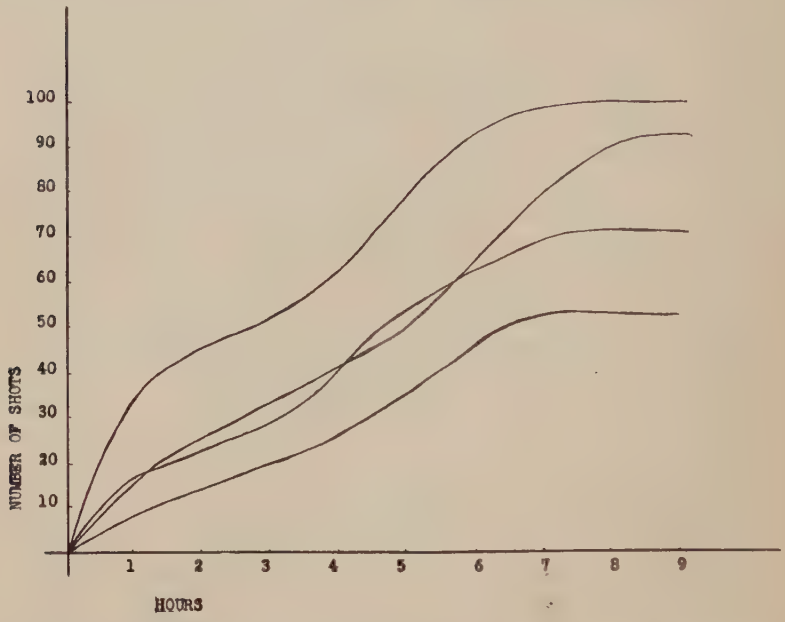

Fig. 5. Smooth curves showing number of shots in vials at successive hours for four plants.

gives a concave curve following the first convex portion. This is followed by a convex curve again indicating the second increase in load. As the number of shots dropped per hour decreases, the curve gradually flattens out until the plant has attained its maximum pulling power. This type of curve was produced in most of the thirty experiments which were performed with the tropograph.

If the weight and the glass tubing be removed from one of these petioles, the petiole immediately bends to the upper side

at a visible rate (plate 31, fig. 4). The force bending the petiole to one side is often sufficient to bring the distal end in contact with the soil (plate 30, fig. 4). In one case the epidermis and cortex were ruptured because of the curvature. If it be first placed erect, the same curvature will occur, but later the terminal portion of the petiole bends upward in response to gravity.

A variation of the turgidity of the cells on the two sides of the petiole doubtless plays an important part in this curvature. That curvature of the petiole of *Podophyllum* may result from a variation of turgor was shown by removing one leaf from fertile shoots. Within less than an hour each shoot had bent over in the direction of the exposed cut surface where the leaf had been removed. The loss of water from the cut surface had decreased the turgidity of the cells on that side sufficiently to bend the distal portion of the shoot to nearly a right angle in some cases. A further indication that osmotic pressure plays an important part in such curvature of stems was obtained by taking a plant after it had curved upon release from the tropograph, peeling off the epidermis from the convex surface, and inverting the petiole in a 10 per cent salt solution. After about an hour the petiole had become straight. When rinsed and placed in fresh water, it again became curved as before. In both of these cases the curvature was brought about by contraction of the one side rather than by an elongation of the opposite side. This would seem to disprove the contention noted in the literature above that geotropic curvature is due to the extension of the lower side, and shows that it is due to a contraction of the upper side.

DISCUSSION

Pressure is known to exert a pronounced influence upon certain phases of growth and upon certain plant reactions, and it has been suggested as a possible cause of other cellular processes. Cell elongation has been shown by Newcomb (1894) to be altered by pressure. Roots encased in casts of plaster of Paris were found to have mature cells much smaller in size than normal cells and with thin walls. Likewise, cell differentiation is altered by pressure, as Pfeffer found in the Windsor bean, where spiral tracheae had developed near the tip of the root, normally developing much farther back. Jeffs (1925), in his study of root-hair formation, regarded pressure as the important factor,

resulting from cellular interaction, in the production of root-hairs. He found that as the sub-epidermal cells of the root ceased elongating, thus checking vertical elongation in the epidermis, lateral evaginations of the epidermal cells due to lateral pressure developed into root-hairs. Farr (1916), in the study of cell-division of the pollen-mother-cells of certain dicotyledons, interpreted quadripartition by furrowing as being influenced by the spherical form of the mother-cells and their loose arrangement in the pollen chamber, the mother-cells thereby being free to undergo such change in volume and form as their internal constitution would favor. In most typical plant cells a cellulose wall opposes change in form and resists increase in volume; hence pressure of the cell content against the wall may account for the formation of the cell-plate.

The present study of the petiole of *Podophyllum* has determined the composite effect of pressure on all of the processes involved in growth and contributes to our knowledge of the physiology of growth by showing the influence of pressure on its rate as well as the energy relations involved both in growth and in tropic responses. It also suggests a means for the investigation of other growth movements which result from stimuli of light, wounding, etc. It gives further light on our knowledge of cellular interaction in the production of mechanical tissue as indicated by increase of strength, and aids in interpreting the responses of plants to movements effected by such agencies as wind and gravity.

It usually has been assumed that pressure decreases the rate of growth. While this is in a sense true, it does not constitute an exact description of the situation. Growth rate might be an inverse function of pressure; yet it is not necessarily proportional to it. The first effect of pressure in all of these experiments was found to be a retardation of growth, and if the weight is not further increased the normal growth rate is resumed. This is seen from the daily records where the first reading following the addition of weight is usually less than subsequent readings until addition of more weight. Thus the first effect of retardation is followed by a stimulation of growth. This is what Hegler (1893) found in the case of tension. At first it might seem that the rate of growth is inversely proportional to the weight, for the curves representing the growth of the plants and

their controls gradually separate. But the fact that this does not continue and that the rate of growth of the plant exposed to pressure may exceed that of the control shows a later stimulating effect of the pressure.

The maximum energy which the petiole of *Podophyllum* with an average diameter of 4.2 mm. at its tip exerts in growth against pressure is that sufficient to sustain a weight of 550 grams. This would be equivalent to 38.75 grams per sq. mm. or a maximum of 3.75 atmospheres. The greatest pressure developed by these petioles is thus less than any of the pressures which Pfeffer found to be developed by roots of *Vicia faba*, which ranged from 5.15 to 19.35 atmospheres. The need for a pushing force by the root greater than that of a stem is obvious from the simple fact that the root must be able to force itself into the soil.

The ability of the petiole to lift a greater load after it had raised a certain weight shows that it increases in strength and points to the probability that additional mechanical tissue is produced. Further evidence of this is to be found in the average increase of 18 per cent in the bending strength of the petioles grown against pressure. These results are not in harmony with those which Pennington (1910) obtained. He found no increase in the bending strength of plants which he subjected to longitudinal pressure, nor could he find any increase of mechanical tissues when studied microscopically. This dissimilarity of results may be due to the use of different plants with apical meristem and to the different methods employed.

That pressure increases the bending strength was also shown in the flexation experiments. In flexation there is produced alternate compression and tension of the tissues on the two sides of the petiole in the plane of flexation. Here the increase in bending strength is about 26 per cent. This is comparable to the average increase resulting from longitudinal compression. Miss Gilchrist (1908), working in a similar manner with sunflowers, likewise found that flexation increased the strength of stems. One important difference is noticed, however. The sunflower stems became stronger in the plane of flexation than at right angles to it, while in *Podophyllum* the strength of the petiole at right angles to the plane of flexation was found to be the greater. In my experiments the difference in the bending strength in the two planes varied all the way from .5 per cent in favor

of the plane of flexation to 46 per cent in favor of the plane at right angles to that of flexation with an average increase of 14 per cent. Miss Gilchrist also found that the diameter was greater in the plane of flexation than in the plane at right angles to it. In my experiments with *Podophyllum* it seems that the diameter of the plane at right angles to that of flexation is larger, which might, in part at least, account for the difference in bending strength in the two directions. Just how this result is produced by the action of bending, it is difficult to say. It may be that the alternate compression and tension permits less deposition of wall material in certain places.

The results of flexation are not necessarily the same as those which might follow the action of wind. Much of the work by others has been more or less confusing for the reason that what have been called wind effects have been merely bending effects. The two may be very different, for the action of wind involves increase in transpiration, which in turn would alter other internal processes that are not affected in such experiments as were performed by Burns (1920), and Gilchrist (1908). Cavara (1912), on the other hand, found that the excessive transpiration accompanying wind resulted in the shortening of the stem and tended to produce the rosette habit. In my experiments the bending did not seem to alter the average length of the petiole; the effect was purely mechanical.

That turgor plays an important part in the raising of the weights of the first group of experiments is doubtless true, but it is doubtful that it is responsible for the increase in strength as determined by the flectometer. If the weight does increase the turgidity of the petiole, then conversely, when the weight is removed, the turgidity should decrease to the normal. It is furthermore not likely that bending back and forth has a pronounced effect upon the turgidity of the tissues. If there were no structural changes produced, there would doubtless not have been such consistent differences in the bending strength in the two directions at right angles to each other as were obtained in these flexation experiments. On the other hand, the bending strength should have been approximately the same in the two directions if turgidity alone accounts for the increase. The structural basis of this increase of strength is further borne out by the microscopic sections of bundles. Ursprung and Blum (1924)

account for all enlargement as a consequence of wall extension and not increased turgor pressure.

The effect of compression in producing increase in strength in the petiole of *Podophyllum* and the production of mechanical tissue supports the contentions of Hartig (1896), Ursprung (1901), and Koehler (1919) as to the formation of "redwood" in conifers, since they attribute the presence of this tissue to an increased compression stimulus on the one side of the stem.

As stated above, Ricome (1920) attributed the geotropic curvature of a stem to compression and tension stimuli. The pressure on the lower side of the horizontal plant acts as a stimulus increasing growth and the tension on the top side decreasing it. If the stem is to curve upward, according to Ricome, as a result of an increase in growth below and a decrease above, then the difference not only must represent a force equal to the weight of the stem which gives rise to the altered growth rates but also must represent an additional force equal to that necessary to bend the petiole. This theory does not coincide with Hegler's (1893) observations on the effect of tension on growth, nor with mine on the effect of pressure. Tension and pressure both seem to retard growth at first. Furthermore, the rupturing of the petiole on the side which was beneath when horizontal indicates that negative geotropism is the result of a contraction of the upper side. This is also borne out by my experiments with the fertile shoots from which one leaf had been removed and with the petiole which was placed in the salt solution.

The weight which the petiole of *Podophyllum* will lift in response to the stimulus of gravity was found to vary from 11.451 to 69.43 grams, with an average of 32.804 grams. To arrive at the total energy of the petiole in our tropograph experiments, we must consider, in addition to the weight which it is sustaining while horizontal, the force which would be required to bend the petiole at right angles. As the petiole is sustaining a maximum weight of 69.43 grams, it has remained straight and still contains potential energy equal to that necessary to bend it. Therefore the total energy of the petiole is equal to the weight sustained plus that required to bend it. From the flectometer records it is estimated that an average weight of 30 grams would be necessary to bring about the bending. Adding this to 69.43 grams would give a total of 99.43 grams as the total energy of the horizontal petiole.

That the force continues to increase for a period of time, as long as 30 hours in some cases, is significant. Schley (1920) found that the osmotic pressure continued to increase until curvature began and then decreased until curvature ceased. It is difficult to understand why this should occur. In the light of my bending-strength determinations, to the effect that the more the petiole is bent the more the force necessary to continue the bending, it would seem that in geotropic curvature, if the force responsible for it is osmotic pressure, then the latter must continue to increase until the petiole is erect and the osmotic pressures of the two sides again become equalized. The tropograph records indicate that whatever the source of the force producing geotropic curvature it increases long after the response begins. In any theory of geotropism this must be taken into account. Not only this but also the manner in which the force increases must be explained. The tropograph records have shown this increase to be periodic, first a rapid increase followed by a less rapid increase, and then a second rapid increase followed by another less rapid rise until the maximum force is developed. In some cases a third increase was found to occur.

These findings are not in accord with the observations of Zollikofer (1918) that the geotropic sensitivity is lost in the dark. If statolith starch disappears in the dark and the responsiveness to the geotropic stimulus decreases, then I am at a loss to explain the continued rise in the force developed in my experiments, for they were performed in total darkness, except for a dim red light when the readings were taken.

If we adopt Němec's theory of geotropism and assume that it is the result of the settling to the bottom of particles within the protoplasm, we can conceive of an increase in this force as taking place with the unequal settling of these particles. The heavier particles will settle first and by their hydrolysis perhaps increase the osmotic pressure below and decrease it above giving the first rise in our curve. Somewhat smaller particles will settle more slowly and while causing the force to continue to increase will probably not cause it to increase at the same rate, accounting for the first concave portion of our curve. The question now arises as to how to account for the second rise and in some cases for the third rise. If it is assumed that the particles are of two or three general sizes or that there is a synthesis

of new particles, the unequal settling of them would give a periodic increase of this force. It seems that even in Small and Rea's theory (1920) of a variable permeability resulting from the differences in potential which follow a "creaming effect" that we must assume that the particles are of several sizes or newly synthesized, thus giving a periodic permeability.

These experiments were conducted in the Plant Physiological Laboratories of the State University of Iowa, and I am greatly indebted to Dr. C. H. Farr for his many helpful suggestions in the prosecution of the work.

SUMMARY

1. The maximum mechanical energy which a plant is capable of expending during growth may be measured by determining the maximum weight which the plant can lift when erect or the force exerted in lifting a weight when horizontal, plus that required to overcome its own rigidity in bending.

2. The maximum weight which a petiole of *Podophyllum* will lift when erect varies from 175 to 500 grams, with an average of 300 grams.

3. The maximum weight which a petiole of *Podophyllum* will lift when horizontal varies from 11.451 to 69.43 grams, with an average of 32.804 grams.

4. The force required to bend the petiole of *Podophyllum* varies from 9.777 to 39.891 grams, with an average of 26.16 grams. For these measurements the number of degrees of the angle of bending of each petiole was ten times the length of the petiole in centimeters.

5. Longitudinal pressure on the apex of an erect petiole results in an increase in the ability of the petiole to overcome such pressure. To lift the maximum weight so applied 10 days are required, during which the weight has been increased by 50 grams daily.

6. Lateral pressure or weight applied to a horizontal petiole of *Podophyllum* increases the ability of the petiole to curve geotropically, overcoming such pressure or weight. To lift the maximum weight so applied, from 6 to 29 hours are required during which the weight has been increased most at first, 13.537 grams per hour, with a second maximum, about 4.5 grams per hour, after about 4 hours. The rate of addition of weight falls

to 2.777 grams per hour after the first maximum and to zero after the second.

7. Pressure on the apex of a petiole of *Podophyllum* results in an average increase of 18 per cent in its rigidity.

8. Flexation—that is, the alternate bending back and forth of a stem-like axis—increases the rigidity of the structure flexed. This increase is less in the plane of flexation, being 12 per cent, than it is in the plane at right angles, in which the increase is 40 per cent.

9. The maximum work which a petiole of *Podophyllum* can do during growth is 1,489,195 ergs in 13 days.

10. In making these determinations the apparatus used consisted of: (a) Sach's auxanometer for measuring growth under longitudinal compression experiments. (b) A flector for accomplishing flexation at a constant rate over a period of several days. (c) A flectometer for measuring the rigidity of a stem, root, peduncle, hypocotyl, or petiole. (d) A tropograph for measuring the maximum force which a stem, hypocotyl, root, peduncle or petiole is capable of exerting during tropic curvature, and the rate of increase of this tropic force if curvature is prevented. The last three pieces of apparatus named were devised especially for this study.

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Explanation of plates

PLATE 30

Fig. 1. Single bundle of plant grown against pressure.

Fig. 2. Single bundle of control plant.

Fig. 3. Another bundle from same plant as in fig. 1.

Fig. 4. Petiole as bent immediately upon release from tropograph and removal of glass tubing.

PLATE 31

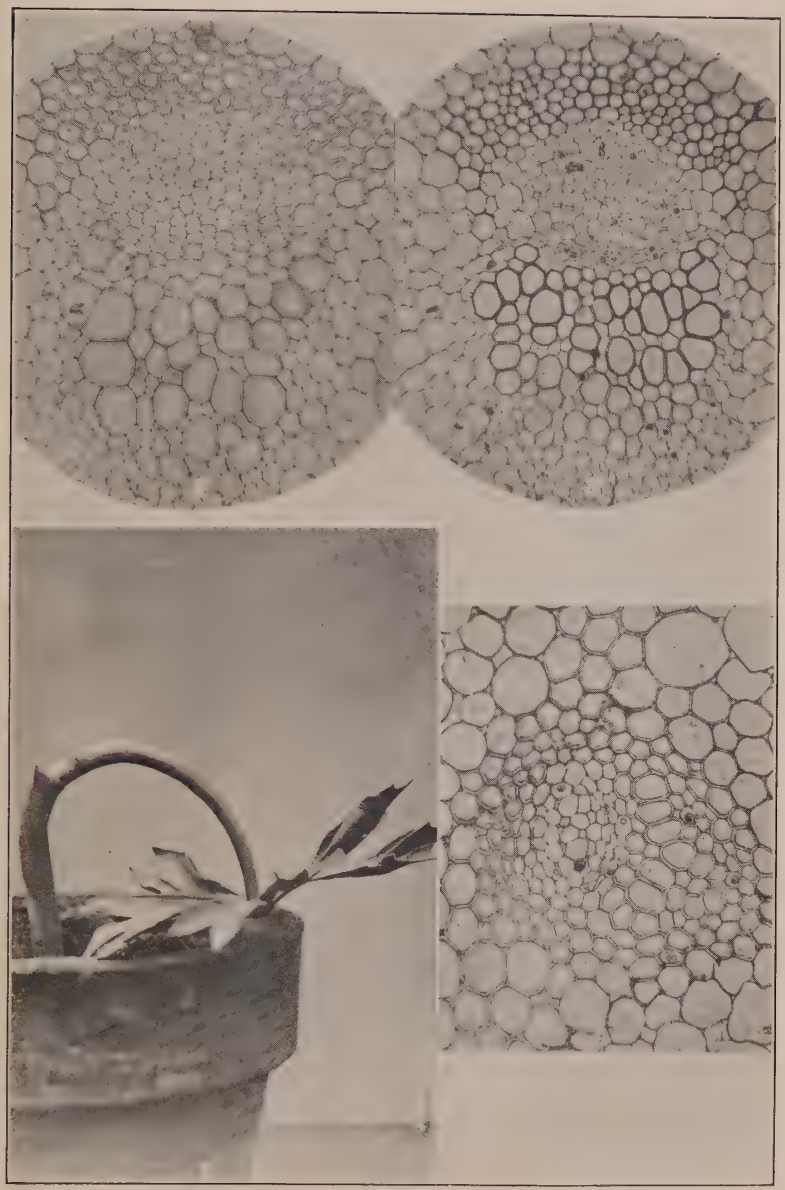
Fig. 1. Plant shown growing against pressure.

Fig. 2. Same petiole as of plate 30, fig. 4, several days later.

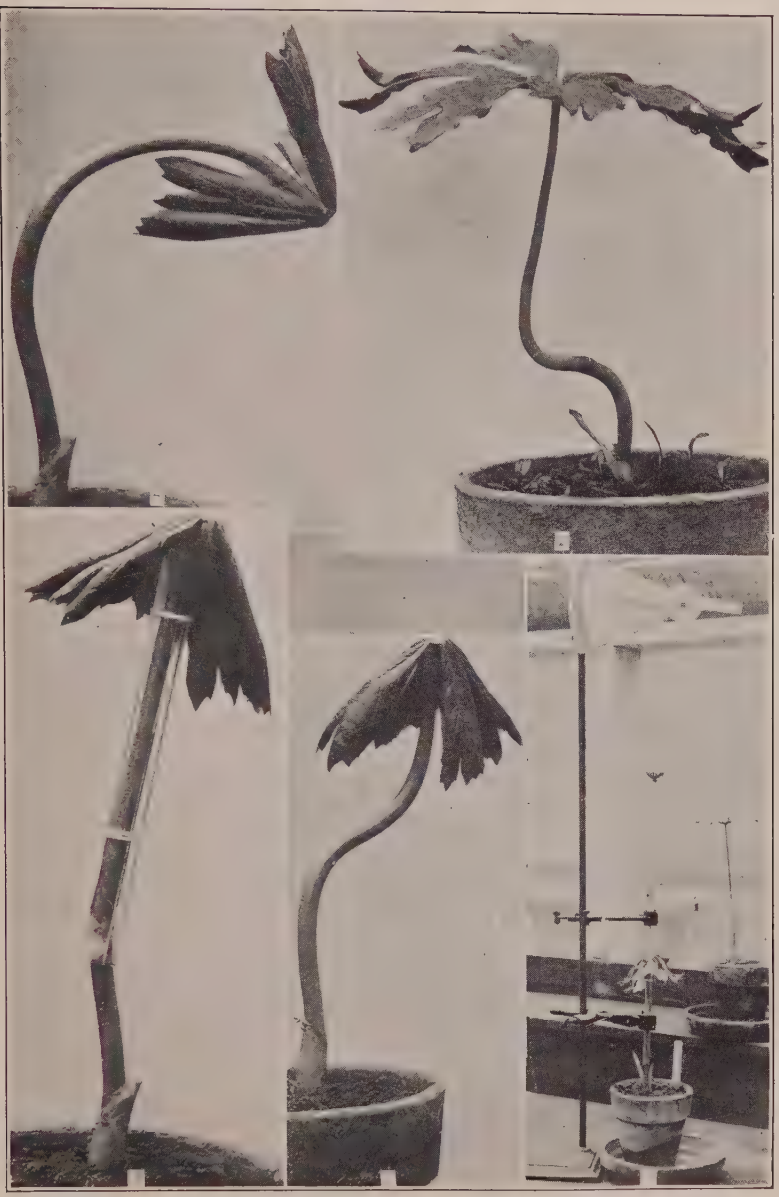
Fig. 3. Another petiole just taken from tropograph and before removing glass tubing.

Fig. 4. Same as in fig. 3 immediately after release from the glass tubing.

Fig. 5. Same petiole two days later.



PODOPHYLLUM PELTATUM



PODOPHYLLUM PELTATUM